REPRODUCTIVE ECOLOGY OF NEW ZEALAND FORESTS: 2. GERMINATION BEHAVIOUR OF SEEDS IN VARIED CONDITIONS

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(Received 13 August 1996; revised and accepted 7 September 1997)

ABSTRACT

Burrows, C. J. (1997). Reproductive ecology of New Zealand forests: 2. Germination behaviour of seeds in varied conditions. *New Zealand Natural Sciences* 23: 53-69.

Freshly-collected seeds of 25 forest species were placed in a variety of conditions and kept, continually moist, in an unheated, partially shaded glasshouse in Christchurch. The treatments were:

1. in fruit tissues.

With fruit tissues cleaned off, then kept:

2. in maximum available daylight;
3. in total darkness;
4. in shallow grooves in soil;
5. air-dry for several months, then moistened;
6. buried five cm below the surface in a cylinder of soil, and where no seedlings had emerged, unearthed after about eighteen months.

Seeds in fruit tissues failed to germinate, or germination success was very low, for 18 species. A further four species had germination success of 36-72% and two species, for which whole fruits are always dispersed, had 90% success or more. Seeds in the well-lit treatment germinated with 90-100% success (with one exception). In the dark, the germination rate was usually slower. Three species failed to germinate, and one germinated poorly. For eleven species the success was 90% or more, and for the rest success ranged from 20%-88%. On soil germination was usually slower and less successful than in the well-lit treatment. Large-seeded species were the most successful. After drying, seeds of six species failed to germinate, and the success for four was below 30%. A further six species germinated with 50-80% success, and for eight species their success was above 90%. In the buried treatment, seeds of eight species germinated and the seedlings died underground. Seeds of twelve species (large-seeded and some smaller-seeded) germinated and sent shoots to the soil surface. A proportion of the seeds of five species germinated, and the seedlings died underground. The remaining seeds went into stasis and these, apparently dormant, germinated when brought into the light, after about eighteen months burial.

KEYWORDS: delayed germination - stasis - habitat variation - diverse behaviour - versatility.

INTRODUCTION

Reproductive processes of seed plants include the following consecutive phenomena: flowering (cone production in gymnosperms), pollination, fruit and seed development, seed storage on parents, seed dispersal, seed storage in the soil and, finally, seed germination and seedling establishment. Vegetative regeneration is important, also, for some species.

A series of studies was initiated in 1985 to investigate the ecology of regeneration processes in lowland forests in the South Island, New Zealand. The reason for undertaking this work was that there is a lack of fundamental information on seed biology in general and the germination requirements of seeds of plants of the native flora in particular. This is abundantly clear from the review by Fountain & Outred (1991) which covered only 38 articles and 113 species.

Aspects of reproductive biology which have been investigated so far during these recent studies include: fruit types and their relationships with dispersal agents (especially frugivorous birds) (Burrows 1994a, 1994b); seed crop sizes (Burrows

1994c); pre-dispersal seed predation (Sullivan *et al.* 1995); seed dispersal (Burrows 1994c, 1996a); seed germination behaviour and seed storage phenomena (Burrows 1989, 1993, 1994d, 1994e, 1995a, 1995b, 1995c, 1995d, 1996b, 1996c, 1996d, 1996e, 1996f, 1996g, 1997); evolutionary determination of aspects of seed biology (Burrows 1994b, 1994e); vegetative regeneration (Burrows 1994e, 1994f).

In Burrows (1997) seed storage was examined in the New Zealand forest context, with the conclusion that a great deal still needs to be known about how seeds behave in nature. Variability of response of seeds to differing experimental conditions is evident but the causes of such behaviour are poorly understood.

The present account describes experiments on seeds of a range of common forest species. Seeds of most of them have already been studied (as outlined in the references on germination behaviour and seed storage noted above). The rationale for conducting further experiments on these species was that only four treatments were used for the earlier tests: standard, in fruit, dark and soil (see Table 1 for details). Two further treatments, dry and buried (Table 1), were tried with most species in an attempt to simulate other conditions which seeds might experience in nature. Also, as the dark treatment in all the tests done in Burrows (1995a, 1995b, 1995c, 1995d and 1996b, 1996c, 1996d) was performed with petri dishes wrapped in aluminium foil, it was necessary that they should be repeated, as it was possible that pinholes had developed in the bent-over foil. Furthermore, it was thought possible that, by using a wider range of treatments, some of the underlying causes of variability of germination response pattern in different seed sets for particular species, as noted in Burrows (1997), might become apparent. This particularly applies to whether an environmental constraint or secondary dormancy may cause delayed germination of seeds in some circumstances.

The specific aims of the work described here were, firstly, to record the behaviour patterns of freshly-collected seeds of a range of common forest plant species in relation to seasonal temperature variations

Table 1. Experimental treatments for the study.

Treatments	No. of replicates of 25 seeds
1. **In fruit** - left in fruit tissues. For all other tests fruit tissues are removed (not completely possible for drupes, achenes).	1 or 2
2. **Standard** - kept wet, on filter paper, in petri dishes, in maximum available daylight.	2 or 4
3. **Dark** - same conditions, but kept in black plastic bags. Checked at about monthly intervals, in a darkroom, under photographic safelight.	2
4. **Soil** - in small grooves in pasteurized potting soil, in small plastic meat dishes, kept continually moist.	2
5. **Dry** - kept dry over winter (3-4 months), then put in conditions as for standard treatment.	2
6. **Buried** - buried 5 cm below soil surface in a plastic drainpipe cylinder 30 cm high. If seedlings do not appear, seeds are unearthed after 1.5 years (approx.) and placed in conditions as for soil treatment.	1 or 2

when they are placed in treatments designed to simulate common field situations. A second aim was to ascertain the potential of seeds of each of the species for storage after dispersal.

MATERIALS AND METHODS

The general methodology was explained fully in Burrows (1995a, 1996e); here it is briefly summarized (Table 1). Ripe fruit were collected from abundantly-fruiting wild parents in forest areas in various parts of the northern half of the South Island (Table 2). The fruit were kept cool in an insulated bin, and the seeds were prepared for the experiments within a few days. As fruit of the species tested ripen at intervals during summer-autumn-winter, the tests for individual species began at various times through this period (Table 2).

One treatment, in fruit, mimics the situation where whole fruit fall from the parents. For all other treatments, to simulate the dispersal process the seeds are separated from the fruit tissues, and these cleaned seeds are soaked in tap water for 24 hours and sorted under a stereomicroscope to exclude damaged or empty individuals. Thus, the seeds being placed in treatments are assumed to be sound and capable of germination. In only a few instances has this assumption been found to be incorrect, when insect larvae or fungi affected the seed contents and were undetected during the sorting process.

Note that most of the species tested are fleshy-fruited, with their seeds dispersed by birds. The few dry-fruited species are wind-dispersed. Some single-seeded dry fruit are achenes and some others are dispersed with the ovary wall intact, as a matter of course. Some fleshy fruit with one or a few seeds (drupes) have part of the ovary wall tightly attached to the seed wall(s), and they too are dispersed as units. They, as well as seeds in the strict sense, are referred to as seeds hereafter in this account.

The standard treatment (Table 1) is a baseline for comparison of results of all other treatments. The best results, in terms of total germination success, are almost invariably achieved in it. This treatment simulates conditions when seeds are released from dry fruit or fleshy fruit are eaten by birds, and the seeds dispersed to reach sites on the ground surface which are moist enough and well-enough lit for germination to take place.

The dark treatment simulates the situation where seeds are dispersed and quickly buried, shallowly, beneath litter. The dark treatment seeds are first monitored when all or most seeds in the standard treatment have germinated. This is to avoid the possibility of initiating germination during the darkroom inspection. As seeds of various species remained quiescent after several inspections it is likely that the methodology is appropriate. If no seeds have germinated in the dark treatment several months after germination is completed in the standard treatment, the seeds are placed in the light to follow their subsequent behaviour.

Both standard and dark treatments are maintained wet on filter paper in petri dishes so that they can be readily observed during monitoring. Nevertheless, they are not sterile cultures, as algae, fungi and bacteria often form colonies in the dishes. These can be introduced during watering. Christchurch tap water is relatively pure, but not chlorinated. They can also be introduced from the air during monitoring and by tiny arthropods such as collembola and fungus gnats (Mycetophilidae) which sometimes enter the dishes.

The soil treatment is kept on pasteurized potting soil in meat dishes with drainage holes. Almost all seeds become at least partly buried by soil, which shifts during watering (performed with a fine spray watering can). The treatment resembles the situation where seeds are dispersed to loose surface soil sites and become partly buried by raindrop or drip disturbance. This treatment probably mimics nature more closely than does the standard because microbes and small arthropods inhabit the soil. However, it is seldom possible to view all seeds and confirmation of germination (usually recognized in petri dishes by swelling of seeds, cracking of seed coats, or change in their colour, as well as radicle emergence) must

Table 2. Germination results for seeds of New Zealand lowland forest species in a range of treatments.

		Standard				Dark
Species; Location; Collection date	**Mean seed weight (g); Fruit type**	**Period before germ. starts (wks)**	**Period over which germ. occurs (wks)**	**% success**	**Germ. rate in relation to standard**	**% success**
Alectryon excelsum	0.23	3	32	56 [+]	slower	20
Banks Peninsula						
E Mar. 1994	F					
Aristotelia serrata	0.004	3	28.5	100	similar	100
Kaikoura						
L Feb. 1994	F					
Beilschmiedia tawa[++]	0.95	5.5	2	100	similar	90
North Marlborough						
M Mar. 1996	F					
Carpodetus serratus	0.00056	4.5	27.5	90	slower	60
North Westland						
M Mar. 1994	F					
Coprosma lucida	0.024	16.5	15	100	similar	94
North Westland						
E Feb. 1994	F					
Coprosma robusta	0.006	2.5	11	96	slower	94
Christchurch						
M Mar. 1994	F					
Cordyline australis	0.008	3	22	98	similar	94
North Westland						
M Mar. 1994	F					
Coriaria arborea	0.0006	1	2	92	–	0
North Westland						placed in light these
E Feb. 1994	F					germinated (80%)
Corynocarpus laevigatus	2.35	<1	21	94	slower [x]	75
Kaikoura						
E Feb. 1994	F					
Dodonaea viscosa	0.0095	1	42	96	similar	88
North Westland						
E Mar. 1994	D					
Freycinetia baueriana	0.00019	14.5	3	92	–	0
North Westland						placed in light these
M May 1994	F					germinated (94%)
Fuchsia excorticata	0.00007	2	5	96	–	0
Banks Peninsula						placed in light these
E Feb. 1996	F					germinated (78%)
Griselinia littoralis	0.034	2	12.5	98	slower	92
Banks Peninsula						
E Apr. 1994	F					
Hedycarya arborea	0.19	11	18	100	slower	100
Kaikoura						
L Feb. 1994	F					

Table 2. Continued.

Soil *			Dry		Buried (5cm) depth	
Germ. rate in relation to standard	% success	No. of months dry	Behaviour when wetted	% success	Behaviour while buried, or when unearthed	% ** success
faster	58 +	5	germinated over 19 weeks	58 +	a proportion germinated and sent shoots to surface over 29 weeks; 40% germinated and seedlings died underground; the rest died	24 +
slower	90	6	germinated over 20.5 weeks	76	80% germinated and seedlings died underground; the rest unearthed in spring 1995 germinated then	20
similar	100	7.5	none germinated, all dead	0	most germinated and sent shoots to the surface in the first year	90
[slower	58]	4.5	germinated over 21.5 weeks	98	all germinated and seedlings died underground	0
slower	80	6	a proportion germinated over 22 weeks; the rest were dead	26	many germinated and sent shoots to the surface over 2 years; the rest died	84
slower	94	7.5	germinated over 14 weeks	72	many germinated and sent shoots to the surface, over 2 years; the rest died	76
similar	90	7.5	germinated over 15 weeks	92	some germinated and sent shoots to the surface, over 2 years; the rest died	48
[slower	93]	6	germinated over 12.5 weeks	90	all germinated and seedlings died underground	0 *
similar	98	5	a small number germinated over 10 weeks	10	many germinated and sent shoots to the surface over one year; the rest died	70
[slower	76]		not done		most germinated and sent shoots to the surface over 2 years; the rest died	90
much slower	12	3.5	none germinated, all dead	0	only a few seeds were recovered; none germinated	0 *
similar	50	6	germinated over 12.5 weeks	94	all germinated and seedlings died underground	0 *
[slower	72]	4	none germinated, all dead	0	all germinated and seedlings died underground	0
slower	86	5	none germinated, all dead	0	all germinated and sent shoots to the surface in second summer	100

Table 2. Continued.

		Standard				Dark
Species; Location; Collection date	**Mean seed weight (g); Fruit type**	**Period before germ. starts (wks)**	**Period over which germ. occurs (wks)**	**% success**	**Germ. rate in relation to standard**	**% success**
Hoheria angustifolia Banks Peninsula M May 1994	0.0024 D	11.5	3	93	slower	88
Kunzea ericoides Banks Peninsula L Apr. 1994	0.000063 D	3.5	11	100	slower	86
Macropiper excelsum North Westland E Feb. 1994	0.0024 F	2.5	7	100	similar	100
Melicytus lanceolatus North Westland M Mar. 1994	0.0036 F	9.5	12	100	much slower [x]	8
Melicytus ramiflorus Banks Peninsula M Feb. 1994	0.0015 F	2	2	100	similar	88
Myrsine australis Banks Peninsula L May 1994	0.014 F	16	41.5	100	much slower [x]	42
Myrtus obcordata Banks Peninsula May 1994	0.0096 F	6	13	92	slower	92
Pennantia corymbosa Kaikoura M Mar. 1996	0.02 F	5	3	94	similar	100
Rhopalostylis sapida North Westland E Feb. 1994	0.17 F	39	5	100	slower	84
Ripogonum scandens Kaikoura L Feb. 1994	0.13 F	7.5	4	100	slower	96
Solanum laciniatum Banks Peninsula E Mar. 1994	0.0017 F	9 [▽]	18	98	much slower [x]	70

Fruit types: F fleshy, D dry. Collection dates: E, M, L. refer to the first, middle and last third of the month.

* those soil treatment results in square brackets are from earlier tests reported in Burrows (1995a, 1995b, 1995c, 1995d, 1996d).

** % germination for the burial treatment is the total success for species where shoots reached the soil surface, or where unearthed seeds germinated.

┼ low, but consistent results for all treatments are due to seed predation by moth larvae (*Conopomorpha cyanospilus*).

┼┼ replicates of 10 seeds only

x dark and soil treatment seeds germinated so late as to indicate that secondary dormancy may have been induced by the conditions (possibly darkness in each case).

◆ a retest is needed to verify that the seeds had died as a direct result of burial.

▽ one precocious seed germinated a few days after the test began.

Table 2. Continued.

Soil *			Dry		Buried (5cm) depth	
Germ. rate in relation to standard	% success	No. of months dry	Behaviour when wetted	% success	Behaviour while buried, or when unearthed	% ** success
slower	84	5	a small number germinated in 6 weeks; the rest dead	16	all germinated and seedlings died underground	0
much slower [x]	76	5	most germinated in 4 weeks	92	all germinated and seedlings died underground	0
slower	86	6	many germinated over 10 weeks	80	44% germinated and seedlings died underground; others unearthed in spring 1995 germinated then	56
much slower [x]	80	4.5	germinated over 23.5 weeks	68	a proportion of the seeds, unearthed in spring 1995, germinated then and over summer; the rest died	52
slower	88	6	most germinated over 11.5 weeks	98	many seeds, unearthed in spring 1995, germinated then; the rest died	76
faster	54	7	all germinated in 27 weeks	100	20% died; many germinated and sent shoots to surface over 1 year; 12% germinated and seedlings died underground	68
[slower	92]	5	germinated over 5 weeks	56	all germinated and seedlings died underground	0
slower	82	7.5	none germinated, all dead	0	most germinated and sent shoots to surface in spring over 2 years	90
much slower [x]	70	8	a small number germinated over 7 weeks, the rest dead	16	most germinated and sent shoots to surface over 2 years	92
slower	84	5	none germinated, all dead	0	all germinated and sent shoots to surface over 2 years	100
slower [x]	56	5	most germinated over 14 weeks	96	all germinated when unearthed in spring 1995	100

await the appearance of shoots.

Mosses and sometimes liverworts colonise the soil treatment trays when seeds are slow to germinate. They are weeded off from time to time.

The dry treatment simulates a situation which, in the New Zealand context, is only experienced, at the most, for a month or two in summer, in the eastern, drier parts of the country. Use of the treatment can be justified by the desire to know whether seeds can be kept in dry artificial storage for a time, and how seeds respond to drying. The seeds are prepared as for those in the stan-

dark treatment, but after cleaning and soaking are dried and kept in petri dishes at room temperature over the winter.

The buried treatment simulates the condition of relatively deep burial of seeds, which probably is an occurrence effected by river siltation, small landslides and treefalls. It differs from the dark treatment in that not only are the seeds in the dark, but they are also almost certainly subject to low oxygen concentrations and higher concentrations of gases such as carbon dioxide, ethylene and methane, than they would experience nearer the soil surface. If no seedlings appear in the buried treatment the tests are maintained for a further year before being unearthed to determine the fate of the buried seeds. Apparently, live seeds are then placed in conditions the same as for the soil treatment and maintained for at least one more year.

Relatively few replicates of the treatments are used. This is partly because of the difficulty of obtaining enough seeds of many species to perform the tests. Seed collecting is the most taxing part of the work. Also, the studies have been in the nature of broad surveys, to discover the basic germination requirements of as many species as possible. The amount of glasshouse space in which to perform the experiments is limited. It was soon found (cf. Burrows 1995a, 1995b) that variability within treatments was almost always low, and this consistency seemed to justify the use of small samples. In a sense every seed constitutes a unit sample. Although only one replicate was used for most buried treatment tests, the results are indicative and often conclusive.

The experiments are conducted in an unheated, partly shaded glasshouse, at the garden area of the Department of Plant and Microbial Sciences, University of Canterbury. Monitoring for all but the dark and buried treatments (see Table 1) is at about weekly intervals, and watering (with tap water) is carried out as necessary. Glasshouse temperatures are recorded. They may rise to maxima of 40°C in summer, but maxima are mainly in the range 15°C-20°C (mean extreme summer maximum 22.3°C, minimum 10.5°C). In winter, temperatures may descend to minima of -4°C, but minima are mainly in the range 5°C-10°C (mean extreme winter maximum 13°C, minimum 1°C). The temperature regime at the Christchurch Botanical Gardens is very similar to that at the University Gardens and its more complete record has been used to compile Figure 1.

Light conditions in the glasshouse have not been measured. Direct sunlight reaches the E-W oriented house only in the early morning and late afternoon in summer. Screening is by a row of evergreen trees, with a few deciduous species, on the northern side. Sunflecks occur on each sunny day and probably reach all parts of the tables. Otherwise, diffuse lighting is experienced through the day.

Siting of the standard, dark, soil and buried treatments is in blocks on tables covered by a sheet of black close-woven plastic mesh (standard, dark) and on a black polythene sheet (soil). The soil and burial test containers have drainage holes and water drains readily from the tables.

Authorities for the plant names are those given by Allan (1961), Moore & Edgar (1970), and Connor & Edgar (1987).

RESULTS

The taxa will be referred to by their generic names, except where two species from a genus were tested. Table 2 summarises the percentage germination success and other relevant data for 25 species for all treatments except in fruit. In that treatment, germination success ranged from nil (for *Beilschmiedia, Carpodetus, Coprosma lucida, Cordyline, Corynocarpus, Freycinetia* and *Ripogonum);* or low (2% for *Griselinia, Hedycarya* and *Rhopalostylis*; 12-24% for *Alectryon, Aristotelia, Macropiper, Melicytus lanceolatus, M. ramiflorus, Myrsine, Myrtus* and *Solanum*); to moderate (36-72% for *Coprosma robusta, Dodonaea, Fuchsia* and *Pennantia*). Only two species, *Coriaria* (with achenes associated with a fleshy corolla) and *Hoheria* (with achene-like fruit having ovary tissues closely investing the seeds), had in-fruit germination of 90% or more.

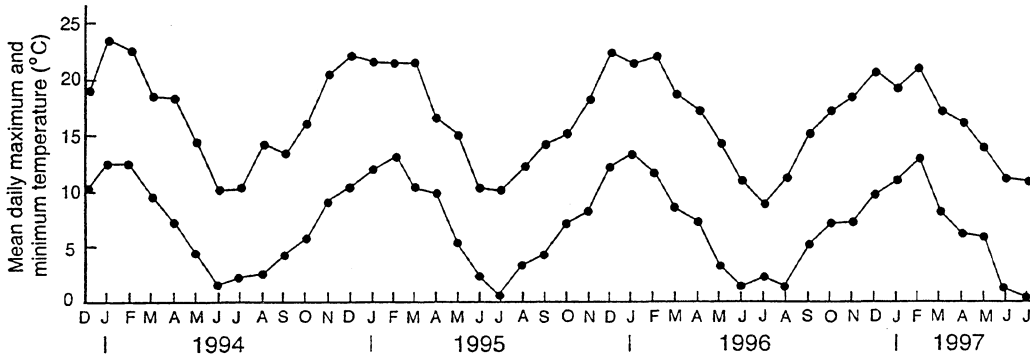

Figure 1. Mean monthly maximum and minimum temperatures 1994-July 1997 for the Christchurch Botanical Gardens Meteorological Station (NIWA 1994-1997).

STANDARD TREATMENT

By contrast, germination success in the standard treatment was between 90% and 100% for all species except *Alectryon.* For that species, the low success is due to the difficulty of detecting dead seeds that had been killed earlier by the larvae of a moth *Conopomorpha cyanospila* (Sullivan *et al.* 1995 and Burrows 1996e). The sorting process screened out insect-damaged seeds of other species (especially *Griselinia, Hoheria, Melicytus ramiflorus, Rhopalostylis),* (Sullivan *et al.* 1995). It also removed seeds affected by fungi (especially *Beilschmiedia*) and empty seeds. The latter are found in all species to some extent, but are moderately abundant in *Fuchsia, Hoheria, Melicytus ramiflorus* and *Myrsine*, and very abundant in *Kunzea.*

The intervals before germination started and during which all seeds in a set germinated are uniquely different for each species. Some seeds of most species germinated in the first six weeks from the start of the experiment (late summer, autumn and winter for the majority of species). Germination began within eight weeks for *Ripogonum* and *Solanum* (with the exception noted in the table). For *Coprosma lucida, Freycinetia, Hedycarya, Hoheria* and *Myrsine* the initial delay was three-four months and, except for *C. lucida* and *Hedycarya*, their germination began in spring. *Rhopalostylis* is outstanding in having had nearly 10 months initial delay.

Species that completed germination of all seeds in a set within two to five weeks of its commencement were *Coriaria, Freycinetia, Fuchsia, Hoheria, Melicytus ramiflorus, Pennantia, Rhopalostylis* and *Ripogonum.*

For most of those species where germination began between February and May, it was completed when temperature was declining (Fig. 1). *Rhopalostylis* had its whole germination period in summer and *Freycinetia, Hoheria* and *Myrsine* germinated when temperature was rising. It is striking that so many of the species examined had at least part of their germination period extending through the winter.

For many of the species tested, germination was spread over 11-22 weeks. Only *Alectryon* (32 wks), *Aristotelia* (28.5 wks), *Carpodetus* (27.5 wks), *Dodonaea* (42 wks) and *Myrsine* (41.5 wks) exceeded that span. In each of these cases most germination was confined to about a one month period, with only a few seeds taking longer to sprout. Reference to Burrows (1997) shows that the period of spread of germination for many species can be very variable among seed sets tested at different times and from different places. Almost all of the species examined here behave in this way, the exceptions being *Coriaria, Fuchsia, Macropiper, Cordyline* and *Solanum.*

DARK TREATMENT

Many seeds of almost all the species tested germinated in the dark (usually more

slowly than in the well-lit treatment). The exceptions were *Melicytus lanceolatus* (with a few seeds only germinating) and *Coriaria, Freycinetia* and *Fuchsia* which failed completely. For the last three, burial in total darkness would be sufficient environmental constraint to maintain their seeds in storage for a time. When they were brought into the light after 6-8 months in darkness, many of the seeds of these species germinated rapidly (Table 2). It would be interesting to know how long they can persist in dark but well-aerated conditions.

If seeds can germinate in the dark, it seems possible that they would also do so if buried. Seedlings arising from seeds that were buried more deeply than the potential maximum length of the extended hypocotyls presumably would die. This would be a hazard for species with small seeds, having limited nutritional reserves. Thus, the lengths of hypocotyls that develop in the dark treatment can indicate the optimum depth for survival of seedlings from buried seeds.

SOIL TREATMENT

Strictly, the consideration of seeds in this treatment should apply only to the species tested in 1994-1996, as the remainder were tested in earlier years under different conditions. However, the results from earlier tests are included here for completeness, and are probably indicative (Table 2). Seeds on soil apparently germinated more slowly than those in the standard treatment (partly an artefact of inability to view every seed during initial phases of germination). Many of them also achieved lower final success than those in the standard treatment. Exceptions to this were species with large seeds: *Alectryon, Beilschmiedia, Corynocarpus, Pennantia* and *Ripogonum.* Reduced success in soil may be because of interference from bacteria, fungi and small arthropods, especially fungus gnats which are glasshouse pests with larvae that may feed both on seeds and young seedlings.

DRY TREATMENT

Seeds which were killed by being maintained air-dry for several months included some of the largest *(Beilschmiedia, Hedycarya, Pennantia* and *Ripogonum*) and smallest (*Freycinetia*). *Griselinia* and *Ripogonum* seeds have very thin seed coats. The other large-seeded species in this category are derived from large drupes. However, their endocarp layers are not particularly thick.

Viability was severely diminished by drying for relatively small-seeded *Coprosma lucida,* and *Hoheria* and large-seeded *Corynocarpus* and *Rhopalostylis*. In a further group of species (*Aristotelia, Coprosma robusta, Melicytus lanceolatus* and *Myrtus*) a moderate to high loss of viability was experienced upon drying of the seeds.

The species with greatest ability to resist drying included one large-seeded species (*Alectryon*) and several with relatively small seeds (*Cordyline, Coriaria, Fuchsia, Kunzea, Macropiper, Melicytus ramiflorus, Myrsine* and *Solanum).* Presumably, their coats prevent water loss and/or their physiology is attuned to resist desiccation, at least for a period.

BURIAL TREATMENT

Three main kinds of response to burial to 5 cm are evident from Table 2. The first is that some seeds appeared to be unable to prevent themselves from germinating when buried and, as the young seedlings have insufficient growth potential to penetrate the thickness of soil above them, they die. However, this interpretation may not be correct for all of the species that failed in the burial treatment because *Coriaria, Freycinetia* and *Fuchsia* seeds survived in the dark treatment. When their buried seeds were unearthed, whole or decayed fragmentary seed coats were found, or sometimes no trace remained. At least for these species, further burial tests are needed to resolve this contradiction.

A second response pattern is that though some seeds die, or germinate and die underground, a proportion of the buried seeds go into a form of stasis (probably secondary dormancy, with some form of metabolic blocking of metabolic processes). A possible trigger for induction of stasis is a relatively low oxygen concentration and increased

concentrations of other gases (*e.g.* carbon dioxide, ethylene) at depth in the soil (Bewley & Black 1982, Corbineau & Côme 1995). The seeds can emerge from stasis when they are unearthed.

In the tests reported here, all species which exhibited this kind of pattern (*Aristotelia, Macropiper, Melicytus lanceolatus, M. ramiflorus* and *Solanum*) have relatively small, but not the smallest, seeds. Seeds from a cohort of any of these species probably can be stored naturally in the soil for at least 18 months. Their behaviour when buried contrasts with that in the standard treatment, which indicated that they lacked primary dormancy. Each of these, except *Macropiper,* is among species which rapidly colonise open, disturbed areas in forest (Burrows 1995a, 1995b, 1996g).

A third type of response is found among the larger-seeded species tested and also among some species with much smaller seeds (*Coprosma lucida, C. robusta, Cordyline, Dodonaea* and *Myrsine).* When buried to 5 cm, their seeds germinate and send shoots to the surface. In the dark treatment, it was evident that each species in this category has the capacity to produce very long hypocotyls. For *Dodonaea* these may be 10 cm or more long.

Many species in this group also have indications of a period of burial-induced stasis for some of their seeds. For *Coprosma lucida, C. robusta, Cordyline, Dodonaea, Pennantia, Rhopalostylis* and *Ripogonum*, emergence of shoots at the soil surface occurred in two episodes in spring-early summer of successive years. *Hedycarya* seeds germinated in the first year, but their shoots did not reach the surface until early summer of the second year (thus surviving in darkness for about 18 months).

DISCUSSION

GENERAL SEED ECOLOGY

Physiological programming of seeds begins while they are on their parents (Gutterman 1992, Wulff 1995) and continues up to the time that they germinate (Bewley & Black 1985). Modifications to the programming occur through the responses of the metabolic processes of the seeds to the complexities of their external environment. According to Baskin & Baskin (1973) and Walck *et al.* (1997) preconditioning (the effect of the environment of the mother plant during seed maturation, affecting dormancy and germination characteristics of seeds) apparently accounts for variations in germination percentages of species between years. Furthermore varied temperatures, light quantity or quality, gas concentrations and moisture conditions either before, or after seeds have ripened, could cause differences in germination times and rates of seeds of the same species from different localities, or even from the same parent at different times through a year (cf. Bewley & Black 1985). For these reasons it is desirable, when trying to discover how seeds of wild plants behave, to begin experiments with freshly-collected seeds, and to use treatments which resemble those that the seeds could experience in nature. It is also desirable not to have preconceived ideas about how seeds will behave based on the experience gained in different environments. Almost all readily available accounts of seed germination and its complexities (*e.g.*, Bewley & Black 1982, 1985, Baskin & Baskin 1989, Mayer & Poljakoff-Mayber 1989, Fenner 1992, Kigel & Galili 1995) arise from experience in the Northern Hemisphere temperate zone. By contrast, relatively few reviews or reference books on the subject have been written for the tropics, subtropics or Southern Hemisphere temperate zone (but cf. Mott & Groves 1981, Foster & Janson 1985, Hopkin & Graham 1987, Putz & Appanah 1987, Garwood 1989, Fountain & Outred 1991, Bell *et al.* 1993, Vazquez-Yanes & Orozco-Segovia 1993, Bannister & Jameson 1994).

PRESENT STUDY

The results from the present study show that individual species respond to varied environmental conditions in diverse ways. Also, different species respond differently, although there are some similar themes. Among the most versatile species that were tested (in the sense that their seeds germinate well after being exposed to a wide

range of conditions) are the widespread and common species *Aristotelia, Coprosma robusta, Cordyline, Melicytus ramiflorus, Myrsine* and *Solanum.* The success of these species can be attributed, in part, to the versatility of the seed phase of their life history. Except for *Melicytus ramiflorus* and *Myrsine* they are well-known as vigorous colonists of disturbed areas. The behaviour of their seeds when buried assists them in performing this colonising role.

Burrows (1997) noted that seeds of many species of New Zealand forest plants tested at different times and from different localities, varied in germination rates and length of the germination period. Such variable behaviour, in at least some of the examples described by Burrows (1997), may be explicable in terms of the results obtained in the present study. It could arise from differences in habitat conditions experienced by the seeds, including physiological programming, or aging while they are still on their parents. However, it could also arise from genotypic differences between individuals or populations.

An evident point is that if germination within a seed cohort is spread over more than a few weeks, individual seeds must be responding differently to prevailing conditions. Seeds for the tests were always collected from a few parents in close proximity. However, all of the species are outbreeders, as far as is known, so free gene exchange and resultant genetic variability is likely, within each local population as well as between populations. Nevertheless, phenotypically-imposed influences from parental hormone systems could also be responsible for some of the variation (cf. Gutterman 1992, Wulff 1995). The full nature and causes of these variable behaviour patterns for any species could be investigated by tests at intervals through a year on seeds from several provenances.

Experiments in well-controlled environments are needed. Among the variables whose effects on seeds need to be examined in a variety of combinations are light intensity, light quality, day length, temperature regime (including day-night variation) and gaseous environment. It is known from studies elsewhere (*e.g.*, Bewley & Black 1982, Baskin & Baskin 1989, Mayer & Poljakoff-Mayber 1989) that interactions between these habitat variables can induce diverse behavioural reactions in seeds.

CORRECTING ERRORS FROM EARLIER RESEARCH

Some misapprehensions that arose from earlier studies on some of the same species as those examined here (Burrows 1995a, 1995b, 1995c) can now be corrected. The new procedure ensuring that the dark treatment seeds are not exposed to light other than the darkroom "safelight" has revealed that *Coriaria arborea* and *Fuchsia excorticata* seeds do not germinate in the dark. In the results reported by Burrows (1995a, 1995c), the seeds of these species must have been exposed to some light through holes in the aluminium foil wrapping.

Another point, reported in Burrows (1995a, 1995b), was that seeds of *Aristotelia serrata, Macropiper excelsum* and *Melicytus ramiflorus* would be unlikely to form seed stores in the soil because their freshly-collected seeds are not primarily dormant and germinate quickly in well-lit, aerated and moist conditions. The present results indicate that each of these species (and also *Melicytus lanceolatus* and *Solanum laciniatum*) is capable of forming seed stores of at least 18 months duration if their seeds are buried to 5 cm depth. This is because numbers of them (ranging from 20% (*Aristotelia*) to 100% (*Solanum*)) went into stasis when buried. It was suggested above that this is a form of secondary dormancy which may be induced by the gaseous environment. Such a cause of secondary dormancy has been described by Bewley & Black (1982). It is significant that only a proportion of the seeds of each of these species, except *Solanum,* is held in stasis when buried. It is uncertain whether the proximate origins of this kind of variable behaviour among seeds in a set are genotypic or phenotypic. In one test by Burrows (1995b) on *Aristotelia serrata* seeds, a small proportion of them germinated much later than the rest (in spring). This may have been another manifestation of the secondary dormancy phenomena, possibly induced by low temperature. Sub-

sequently, in tests on this species reported in Burrows (1997), different provenances of seeds have behaved very differently (one set having all seeds germinate within a month of being placed in the experiment).

OTHER RELEVANT STUDIES

Ogden (1985) suggested that *Fuchsia excorticata* seeds probably have long-lived seeds in storage because of its prominence in samples of surface soil incubated in a glasshouse. Experiments described here, on germination of the seeds of *Fuchsia, Freycinetia baueriana* and *Kunzea ericoides* after burial for about 18 months, have not borne out the view that these species could persist for more than a few months in soil storage, although Sem & Enright (1996) found that a few *Kunzea* seeds germinated in soil in which influx of new seeds had been prevented for 15 months. This contrasts with the relatively large number of *Kunzea* seedlings which emerged in soil trays that received the current year's seedfall. In a similar study near Auckland, Enright & Cameron (1988) found that many *Kunzea* and *Cordyline* seeds but only rare *Myrsine australis* and *Fuchsia* seeds germinated from sites protected from seed influx for two years.

No *Coriaria, Freycinetia* or *Fuchsia* seeds germinated from the covered sites, in Sem & Enright's (1996) study, after 15 months, although their seeds were represented in the current seedfall, and germinated in soil trays after no more than a year. Nevertheless, in the present study, the ability of the seeds of these three species to remain alive after being kept moist and in the dark for about nine months, suggests that it is possible that they could form natural seed stores in the soil for at least that long, and probably longer.

Other species which were shown to be capable of being stored for a time (constrained by the experiment to be no longer than a year), in Sem & Enright's study, were *Carpodetus serratus, Cordyline australis, Melicytus ramiflorus* and *Rhopalostylis sapida.* In contrast, seeds of *Kunzea, Melicytus ramiflorus* and *Rhopalostylis* germinated in soil trays in the field within a month. These apparently contradictory results are consistent with the range of results for the respective species in the present study (and those reported in Burrows 1977). Conditions at Sem & Enright's field site, near Auckland, are considerably warmer than those where the present study was done, in Christchurch. Also, their glasshouse was warmer than their study site, so temperature differences probably account for timing differences in the two studies.

Contrasting with their behaviour in the present study (sprouting to reach the soil surface after having been buried to 5 cm depth), seeds of *Cordyline australis* and *Myrsine australis* apparently remained in stasis in soil for two years in the situation described by Enright & Cameron (1988). Possibly some aspect of the respective temperature regimes also caused these differences in behaviour. The Christchurch glasshouse extreme temperature range (including the peaks of high temperature) will be greater than that beneath a forest canopy in Auckland, though mean temperatures will be higher in Auckland than in Christchurch (Garnier 1958). It is also likely that genetic differences affect seed behaviour for species found in Auckland and the mid-South Island.

Various other studies have examined aspects of seed germination behaviour which are relevant, in part, to the present work. The adverse effect of drying on viability of *Corynocarpus* and *Griselinia littoralis* seeds was described by Simpson (1979) and Bannister *et al.* (1996). *Corynocarpus* is more resistant to drying. Similar information was noted for *Beilschmiedia tawa* by Knowles & Beveridge (1982) and for *Ripogonum* by Macmillan (1972).

In Sem & Enright's Auckland study of the potential of seeds for being stored in soil the lack of primary dormancy, at least in a proportion of the seeds of certain species, was mentioned earlier. Enright & Cameron (1988) had earlier noted the relatively rapid germination of *Kunzea* and *Rhopalostylis* seeds in Auckland.

Moderately long periods for germination of sets of seeds (in some cases with a few individuals germinating relatively quickly) were noted for *Dodonaea* and *Pennantia* by

Hocking (1935) (Wellington). Similar observations were made for *Alectryon, Beilschmiedia tawa, Cordyline australis, Corynocarpus, Griselinia littoralis* and *Hedycarya* by Platt (1987) (Auckland).

Seeds which they thought needed a light stimulus for germination and which sprout after soil disturbance were noted by Enright & Cameron (1988) and Partridge (1989) (*Carpodetus, Coprosma lucida, Cordyline, Hedycarya* and *Melicytus ramiflorus)*. However results in the present study indicate that darkness is not the only factor involved in germination inhibition of these species. Fountain & Outred (1991) suggested that seeds which respond positively after soil disturbance are probably coming out of dormancy in response to a light stimulus. This is consistent with some conclusions from the present study, but is yet to be proven conclusively.

There is little definite evidence on the need for chilling of New Zealand seeds to promote germination (but cf. Haase 1987 and Keogh & Bannister 1992). Chilling might hasten germination of, *e.g. Coprosma lucida, Hoheria, Melicytus lanceolatus, Myrsine* and *Solanum* seeds. Rigorous testing of this point is needed.

CONCLUSIONS

Some interesting seed germination behavioural patterns are exhibited among the species that were tested. The results are more in the nature of natural history observations than deep science. However, these observations are an important part of the process of scientific enquiry for, using the information that arises from them, it is now possible to begin to ask the appropriate questions and to design the appropriate experiments to test the questions. One clear indication is that the seeds of many of our forest species have less in common with seeds of Northern Hemisphere temperate zone forests than they do with seeds of subtropical, or tropical forests in Queensland (cf. Hopkins & Graham 1987) or perhaps the Solomon Islands. This is why we need to develop our own concepts for use in seed biological studies and rely less on the literature on the subject that is based on Northern Hemisphere temperate zone models (cf. Burrows 1994d).

ACKNOWLEDGEMENTS

Thanks are due to Nancy Goh for typing, Lee Leonard for the diagram, and to the Lottery Grants Board and J.S. Watson Research Trust, Royal Forest and Bird Society, for funds which made this research possible.

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